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PALEONTOLOGY.—*The classification of the strophomenoid brachiopods.* ALWYN WILLIAMS, Glasgow University. (Communicated by G. A. Cooper.)

The strophomenoid brachiopods include a host of diversified stocks that flourished mainly during Paleozoic times, although a descendant, the thecideid *Lacazella*, still survives. The morphological variation of the group is extremely wide, as a comparison of such bizarre forms as *Gemmellaroia*, *Leangella*, *Scacchinella*, *Stropheodonta*, *Thecospira*, and *Taffia* shows. Nevertheless, there are a number of morphological features that may be regarded as typically strophomenoid; they include the pseudopunctate condition of the test, the shell modification due to the loss of a functional pedicle, the presence of a pseudodeltidium and chilidium, the nature of the cardinal process and the absence of brachiophores, and shell convexity.

The pseudopunctae represent long, unbranched, arcuate calcareous rods embedded within the fibrous layer of the shell (Fig. 1). They do not penetrate the lamellar layer, and it is supposed that they were laid down by the outer epithelial layer of the mantle immediately behind the outer lobe. It is probable that the deposition and growth of these spicules were limited mainly to the mantle proper, for in the postero-medial portion of the adult shell, an area presumed to have been occupied by the viscera, an inner impunctate fibrous layer generally extends over a pseudopunctate zone laid down during the early stages of shell growth. In addition, the structures grouped around the notothyrium—the cardinal process, socket ridges, and notothyrial platform—are impunctate, as are also the teeth and supporting lamellae of the pedicle valve; although in the stropheodontids, which had a series of denticles arranged along the hinge-line in place of simple

teeth each denticle is built of fibrous material deposited around a rod of nonfibrous calcite similar to the pseudopunctae. The chilidium and pseudodeltidium are also impunctate, being composed principally of an extension of the lamellar layer sometimes supported by an underlying deposit of fibrous calcite. Beecher (1901), p. 260) cited the impunctate nature of the pseudodeltidium as evidence to support his contention that the pseudodeltidium represents a third shell subsequently fused to the pedicle valve in contrast to the punctate deltidium, which he regarded as an integral part of the pedicle valve, in punctate telotrematous forms. In this respect at least his observations are incorrect: the pseudodeltidium is impunctate because it is composed of the lamellar layer which is not perforated in any strophomenoids, whereas the deltidium of such a form as a terebratuloid is punctate because both fibrous and lamellar layers of the shell are penetrated by the caecae.

It has long been known that in the post-nepionic stages of the majority of strophomenoids a functional pedicle was absent and that consequently the mode of life varied from lying free on the sea floor to attachment either by the pedicle or by cementation of the pedicle valve to some foreign body. The persistence of a functional pedicle throughout life is more characteristic of the earlier strophomenoids for, despite exceptions like *Leptaena*, most of the later Lower Paleozoic stocks were not attached. Attachment by cementation of the pedicle valve was a later development attained by many independent groups but especially characteristic of the Upper Paleozoic orthotetaceids.

The position of the pedicle in relation to

the valves is a highly distinctive feature of the strophomenoids. In the young stages of unattached stocks like *Sowerbyella*, *Fardenia*, and *Strophomena*, as well as in forms with a persistently functional pedicle like *Leptaena*, the pedicle base was ensheathed in a pipe consisting of an extension of the lamellar layer situated on the apex of the umbo and not on any part of the interarea of the pedicle valve. This pedicle sheath then was distinct from the pseudodeltidium or delthyrium as can be seen in adult forms with the scar of the pedicle sheath still visible, though in some strophomenoids with a persistent pedicle the foramen was frequently enlarged by resorption and encroached on to the apex of the pseudodeltidium.

The disposition of the pedicle sheath represents a radical departure from the telotrematous pedicle opening which is limited to the delthyrium. Also if Percival's observation (1945) on *Terebratella inconspicua* Sowerby—that the pedicle valve occupies a dorsal position during development—had general application the position of the pedicle foramen has an added significance, for the inclination of the sheath away from the hinge-line suggests that in this group the converse was true.

The limitation of the pedicle opening to the apex of the pedicle valve and not to the interarea probably accounted for the complementary growth of the pseudodeltidium and chilidium: the latter structure is an integral part of the brachial valve yet it fits snugly with the edge of the former and its size is inversely proportional to the development of the pseudodeltidium. In this way the median openings of the interareas which in other brachiopods accommodated the pedicle were effectively sealed by the mantle flaps which were also responsible for the growth of the interareas. This complementary growth of the pseudodeltidium and chilidium was expressed in the more advanced stocks such as the stropheodontids and orthotetaceids in a trend toward the complete elimination of the chilidium and the development of an entire pseudodeltidium flush with the hinge-line. This ultimate stage was reached independently by many Devonian stropheodontids but only by one orthotetaceid, the Triassic *Thecospira*, for

even in the Permian forms like *Meekella* and *Derbyia* a vestige of the chilidium remained and the pseudodeltidium carried a narrow median fold which accommodated it. Nevertheless, despite such a trend and its culmination in the stropheodontids and *Thecospira* it is true to say that both structures are typical features of strophomenoid organization.

The development of two distinctive types of cardinal processes is also highly significant in the strophomenoids.

In a number of early stocks like *Taffia* and *Leptella* the diductor scars must have been attached directly to the floor of the notothyrium for there are no outgrowths which could have accommodated the muscle bases.

The most primitive modification of this state was the growth of a median partition which usually extended from the notothyrial floor to the chilidium as in the plectambonitids. This septum is commonly described as a simple cardinal process and the continued usage of this term is eminently convenient but in all probability the diductor bases were attached to the notothyrial floor on either side of the median septum or to a pair of small lateral ridges.

A similar development occurred in the leptestiids. Thus some early members like *Leptella* were without a median partition while some later stocks like *Leangella* were equipped with a series of lateral ridges in addition to the median septum. The leptestiids were characterized especially by the development of a pair of prominent plates—the chilidial plates—forming the lateral walls of the notothyrium. These together with the median septum were not only firmly ankylosed to the notothyrial floor but also elevated above the hinge-line and prolonged ventrally to it and since the muscle bases were probably inserted within the slots formed by the median septum and the chilidial plates the entire structure is analogous to the bilobed cardinal process.

The bilobed cardinal process of the strophomenaceids and orthotetaceids is quite distinct from the plectambonitaceid arrangement for the diductor muscles were attached not to the notothyrial floor but to a pair of outgrowths from it, each of which bore

the muscle bases on the posterior face, the area of attachment being often increased by the growth of numerous thin calcareous plates. Öpik (1932, p. 61) has commented on the presence of a fine ridge lying medianly between the lobes of the cardinal process of many strophomenaceids and his suggestion that this ridge is a degenerate homologue of the plectambonaceid median partition is probably true.

Despite subsequent modification of the

strophomenaceid cardinal process, as for example the stropheodontids and orthotetaceids in which the chilidium and notothyrium are vestigial or absent and the cardinal process lobes project for some distance into the umbonal region of the pedicle valve, the pattern of development outlined above seems to be fundamental.

Another important feature of strophomenoid organization was the apparent, and in many stocks the undoubted, absence of

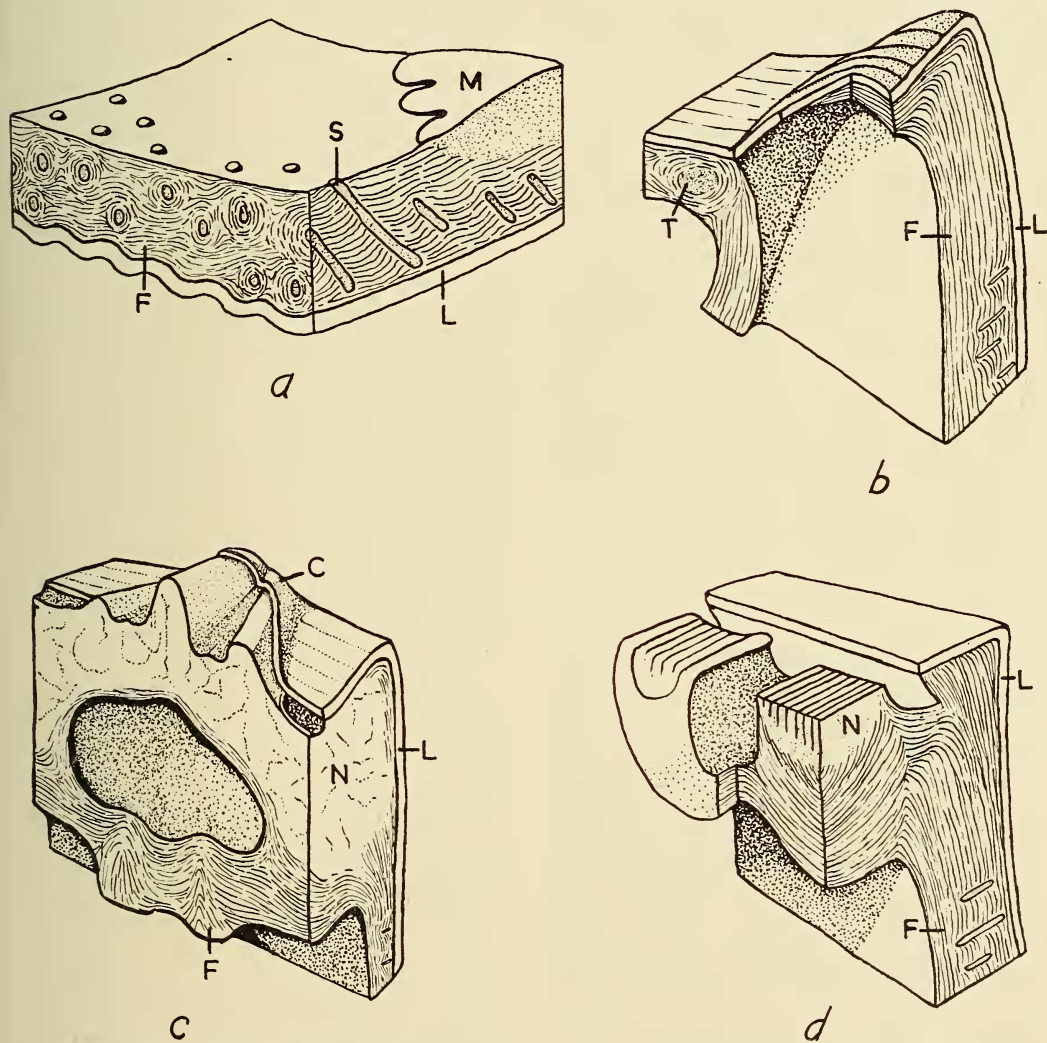


FIG. 1.—Strophomenoid shell structure: A, Diagrammatic representation of a portion of a strophomenoid valve just anterior to the muscle scar showing the lamellar layer (L), the spicules (S) embedded in the fibrous layer (F), and the nonfibrous calcareous deposit of the muscle base (M); B, structure of the strophomenoid pseudodeltidium showing the lamellar layer (L), the fibrous layer (F), and a section of a tooth (T); C and D, the plectambonaceid and strophomenaceid cardinal processes, as typified by *Sowerbyella* and *Strophonelloides*, respectively; chilidium (C), lamellar layer (L), fibrous layer (F), and calcareous nonfibrous deposit (N).



any specialized structures associated with the cardinalia which gave support to the lophophore. Thus in the stropheodontids the pair of ridges forming the inner boundary of the sockets in early members are usually referred to as "brachiophores." With the progressive spread of denticles along the hinge line in later stocks, the teeth and socket arrangement became vestigial and the ridges either disappear entirely or, exceptionally as in the Leptostrophias, became modified to form ankylosed buttresses to the cardinal process lobes. It seems then that the ridges were nothing more than internal walls to the sockets, and the function of lophophore support cannot be ascribed to them. This is equally true for the strophomenids which are equipped with weak ridges like the early stropheodontids.

Within the orthotetaceid group there is also no evidence to suggest that any specialized structures supported the lophophore; the presence of strong, large teeth, the loss of the interarea of the convex brachial valve, and the pronounced ventral growth of the bilobed cardinal process all contributed to the development of a pair of highly modified socket ridges which usually formed concave cups ankylosed to the sides of the cardinal process lobes and supported by a pair of plates growing up from the floor of the valve, e.g., *Meekella*. Even in *Thecospira* the calcareous spires were not attached to any structures associated with the socket ridges but were supported by a pair of very short, scarcely differentiated outgrowths from the bases of the cardinal process lobes.

Öpik (1933, p. 44) has come to a similar conclusion in his investigation of *Leangella* in which the ridges defining the teeth sockets are especially prominent; and in the plectambonaceids generally it is highly likely that the so-called "crural processes" or "brachiophores" functioned only as socket bounding ridges. It is therefore suggested that the term "socket ridge" be used in place of "crura" or "brachiophores" for all strophomenoids.

There is not very much evidence as to the form of the strophomenaceid lophophore but from a knowledge of occasionally preserved impressions as in *Leptaenisca* and

"*Strophomena*" *jukesi* Davidson it is probable that it consisted of a pair of depressed spiral coils, a disposition compatible with shell configuration.

A spirolophous lophophore was apparently also characteristic of the orthotetaceids; impressions of depressed coiled brachia are found in *Davidsonia* and in *Thecospira*, a form hitherto classified as a rostrospiraceid, the fleshy brachia were strengthened by the development of a pair of spirally coiled calcareous ribbons. These spires form a pair of high cones extending well into the interior of the pedicle valve and it is probable that the lophophore of those orthotetaceids in which the depth of the shell was greatly increased by the exceptional growth of the pedicle valve were similarly disposed.

On the other hand many paleontologists, notably Kozłowski (1929) and Öpik (1933), have concluded that the strongly elevated and striated ridge often found in the plectambonaceid brachial valve completely surrounding the postero-median area (here called the "lophophore platform") represent the zone of attachment for the lophophore in a manner analogous to the lophophore-supporting structure of thecideids. The suggestion is certainly the most plausible explanation for the development of such an extraordinary feature and if it is correct the lophophore probably consisted of a simple lobate ring (compare the ptycholo-phous condition as in *Lacazella*).

Elevated ridges are also found in the brachial valve of the strophomenaceid *Christiania* and are strongly reminiscent of the plectambonaceid lophophore platform. In this stock however the partitions are disposed in two discrete loops and if the functional interpretation of these structures is correct the lophophore was schizolophous.

One other important characteristic remains to be discussed—namely, the configuration of the shell. The protegulum and nepionic shells of all strophomenoids, as far as known, were biconvex, a relationship that was maintained throughout the ontogeny of the orthotetaceids except for a minority like some schellwienellas in which the pedicle valve became concave during ephebic stages of growth.



The brachial valve of all strophomenaceids and plectambonaceids in contrast became concave in neanic stages at least and although many independent stocks develop resupinate shells the concavo-convex relationship of the neanic stage was never completely eliminated.

This contrast between the biconvex shell of the orthotetaceids and what is essentially a simple or modified concavo-convex shell of the plectambonaceids and strophomenaceids was probably accompanied by important differences in anatomical distribution and constituted a significant divergence within the group.

#### THE BASIS OF CLASSIFICATION

Until the publication of Öpik's brachiopod studies (1930-1934) the classification of the strophomenoids had never been in a satisfactory state although their distinctiveness had been apparent to paleontologists since 1848 when King took what was then a radical step and erected a family, the Strophomenidae, for the inclusion of *Strophomena* and allied forms. Even the historic studies of Beecher did little to stimulate any worthwhile suprageneric grouping and as recently as 1929 Schuchert and Le Vene (p. 16) described the classification of the strophomenoids as "not yet satisfactory" and were content to use resupination as a subfamily division of the Strophomenidae though they must have been aware of the artificiality of such an arrangement.

The plectambonaceid classification proposed by Öpik is preeminently utilitarian; it consists of the grouping together of demonstrably related genera into subfamilies, families, etc., by purely morphological comparisons: but because it is executed with all due regard to the range of individual stocks it transcends the pigeonholing of genera and allows for the establishment of as natural a classification as one can expect in the light of present knowledge.

The building up of a classification from a series of basic units in this way reveals a number of important features concerning the morphogeny of a series of related stocks. It is for instance usual to find that very few, if any, characters are peculiar to a group; many characters, often the most diagnostic

ones, appear independently in other remotely related stocks and it appears that the higher the suprageneric category the greater the morphological overlap with other categories.

Thus superfamily definitions of plectambonitaceids and the orthoid clitambonaceids classified in this way are virtually the same although nobody acquainted with the groups would hesitate to agree that they were independent of each other from inception to extinction.

This continual reduplication of morphological features in undoubtedly independent groups is of course related to the mechanics of evolution. It is an expression of parallelism in related stocks and though it raises many taxonomic problems it cannot be ignored. This realization should allay most doubts arising from a classification in which it is sometimes impossible to describe a series of characters which are unique to one category or another.

Another fact emerging from the building up of a classification by the grouping together of related genera is that any morphological features will generally have a taxonomic importance directly related to the number of independent lines of descent (expressed systematically as genera) constituting a stock and not a preconceived value constant throughout a series of stocks. For example, the type of cardinal process is taxonomically one of the most important strophomenoid characters. Along with other features it serves to distinguish the plectambonitaceids from the strophomenaceids and in this instance has a superfamily status. In contrast, the absence of a cardinal process in the taffiids and leptestiids serves only to distinguish genera although had such primitive stocks undergone persistent divergences and specialization unaccompanied by the development of a cardinal process its absence would have been correspondingly more important taxonomically.

This is true for instance of the orthotetaceids. The orthotetaceids were equipped with a bilobed cardinal process homologous with the strophomenaceid one, and on the basis of this structure alone would be included within the strophomenaceids. But

the orthotetaceid stock, which was distinct in such features as the persistence of a bi-convex shell throughout ontogeny and the almost universal adoption of the cementing habit, survived into the Trias and during its existence underwent a number of significant divergences some of which merit family recognition, thus imparting to the stock a superfamily status. Accordingly the bilobed cardinal process being present in all members of the Strophomenacea and Orthotetacea has a subordinal value.

This pattern of variable taxonomic values for the cardinal process is true for all characters and is a natural manifestation of divergence and development.

The classification proposed below has been modelled with the foregoing considerations in mind. Its basic units—the generic stocks—have been grouped together into appropriate suprageneric categories and the only factor other than morphological comparison which has been given particular attention is the time range of each genus, in the hope that the more blatant deficiencies of morphological grouping will be eliminated.

#### Suborder STROPHOMENOIDEA Öpik, 1934, emended

Brachiopods derived out of orthoid ancestors by the development of a pseudopunctate shell and by the early loss of a functional pedicle so that the majority of forms included in the suborder either lay free on the sea floor or were attached by cementation to a foreign body; delthyrium and notothyrium closed posteriorly by the complementary development of a pseudo-deltidium and chilidium; diductor bases of the branchial valve attached to a bilobed cardinal process or to the notothyrial floor variously modified and usually divided into two distinct areas by a median "cardinal process"; lophophore, unsupported by any specialized part of the cardinalia but in some stocks presumably attached to a platform developed on the brachial valve and exceptionally strengthened by a calcareous skeleton, generally spirolophous, sometimes ptychlophous, exceptionally schizolophous. Lower Ordovician to Recent.

#### PLECTAMBONACEA, n. superfamily

Concavo-convex or resupinate strophomenoids with cardinalia consisting of well developed socket ridges, a notothyrium covered by a

convex chilidium sometimes supported, and exceptionally replaced, by a pair of chilidial plates, and a cardinal process, which when present, consists of a simple median ridge with subsidiary lateral ridges in later forms; pseudo-deltidium small, pedicle presumably functional in those adult forms with a persistent supra-apical foramen, more usually lost during ontogeny so that mature shells of most stocks were unattached. Ordovician to Devonian.

#### Family Taffiidae Ulrich and Cooper, 1936

Plectambonaceids with orthoidlike musculature and cardinalia; notothyrium covered completely by a convex chilidium, cardinal process when present, simple, median supra-apical foramen small, persistent throughout ontogeny. Lower Ordovician, Upper Canadian to Chazy. Type genus, *Taffia* Ulrich.

#### Family Plectambonitidae Kozłowski, 1929

Plectambonaceids with a median cardinal process growing from the notothyrial floor and ankylosed posteriorly to a convex chilidium; pedicle valve with a pair of accessory teeth lying anterolaterally to two simple teeth; brachial valve with a variably developed lophophore platform; supra-apical foramen sporadically persistent in adult forms. Lower and Middle Ordovician.

#### Subfamily Plectambonitinae Jones, 1928

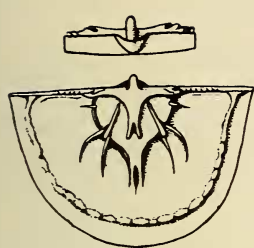
Plectambonitids with a denticulate hinge line in addition to the accessory and simple teeth; pedicle valve with divergent diductor scars separated anteriorly by a low broad plate; brachial valve with aseptate muscle scars. Lower and Middle Ordovician (B<sub>2</sub> to C<sub>3</sub> of the Baltic.) Type genus, *Plectambonites* Pander.

#### Subfamily Ahtiellinae Öpik, 1933

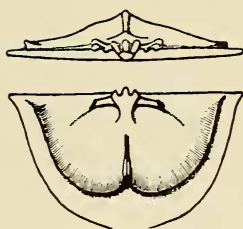
Plectambonitids with smooth hinge lines and a lophophore platform developed on the brachial valve. Lower Ordovician (B<sub>3</sub> to C<sub>1</sub> of the Baltic.) Type genus, *Ahtiella* Öpik.

#### Leptestiidae, n. family

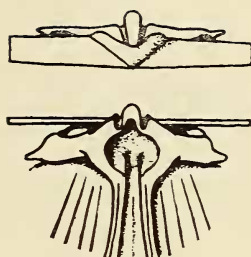
Plectambonaceids with a pair of chilidial plates usually supporting a chilidium forming the sides of the notothyrium and generally ankylosed to the median cardinal process to form a tripartite structure; brachial valve usually provided with an elevated lophophore platform. Lower Ordovician to Middle Devonian.



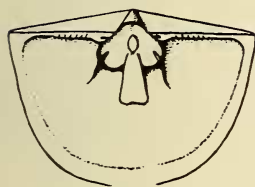
2a



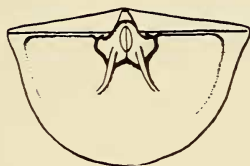
3a



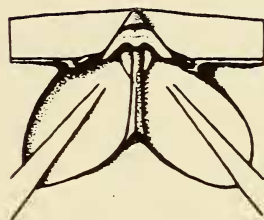
4a



2b



3b



4b



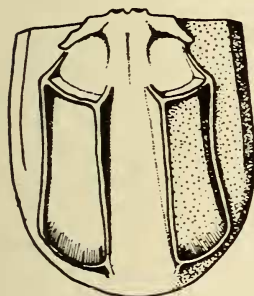
5a



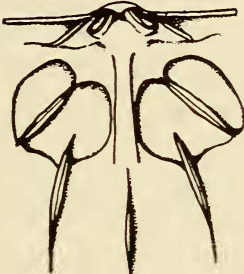
6a



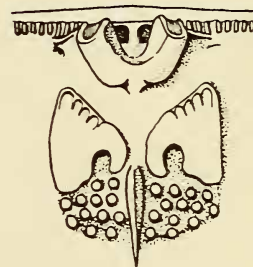
7a



5b



6b



7b

FIGS. 2-7.—2, Plectambonitid morphology, *Ingria* Opik; interior of brachial valve (2a) with posterior view above; interior of pedicle valve (2b). 3, Leptestiinid morphology, *Leptellina* Ulrich and Cooper; interior of brachial valve (3a) with posterior view above; interior of pedicle valve (3b). 4, Sowerbyellinid morphology as typified by *Sowerbyella* Jones; cardinalia of brachial valve (4a) with posterior view above, posteromedian area of pedicle valve (4b). 5, Christianiid morphology as typified by *Christiania* Hall and Clarke; interior of brachial valve (5a) with posterior view above, interior of pedicle valve (5b) with the anterior part of the shell removed to show the posteromedian area. 6, Generalized strophomeninid morphology; cardinalia and muscle scars of brachial valve (6a) with posterior view above, posteromedian area of pedicle valve interior (6b). 7, Stropheodontid morphology, *Strophonelloides* Caster; cardinalia and muscle scars of brachial valve (7a) with posterior view above, posteromedian area of pedicle valve interior (7b).



## Subfamily Leptestiinae Öpik, 1933

Leptestiids with the socket ridges not fused with the chilidial plates and with a strongly developed lophophore platform; median cardinal process occasionally absent, in some later stocks flanked by two or more subsidiary ridges; adductor scars of brachial valve sometimes borne on an elevated platform lying anterior to the cardinalia; accessory teeth and denticulate hinge-line occasionally developed; supraapical foramen never persistent throughout ontogeny. Lower Ordovician (Upper Canadian) to Upper Silurian. Type genus, *Leptestia* Bekker.

## Subfamily Sowerbyellinae Öpik, 1930

Leptestiids with the chilidial plates, median cardinal process, and socket ridges ankylosed to the notothyrial platform to give a structure like an inverted V; hinge line exceptionally denticulate or pierced by oblique canals; apical foramen rarely persistent throughout ontogeny. Ordovician to Middle Devonian. Type genus, *Sowerbyella* Jones.

*Discussion.*—The leptestiinids and the sowerbyellinids were from their inception quite distinct from contemporary plectambonaceids especially in the development of the chilidial plates and it seems that the two groups represented an important divergent development from the strophomenoid ancestral stocks.

Ulrich and Cooper (1936, p. 626) erected a subfamily, the Leptellinae, for the inclusion of early forms like *Leptellina* and *Leptella* which had either a simple cardinal process or none at all. In the opinion of the writer the subfamily is best regarded as a synonym of the Leptestiinae Öpik, 1933; many European leptestiinids also possess a simple median cardinal process and its absence in *Leptella* was, as Ulrich and Cooper demonstrated for the taffiids, not particularly significant among primitive plectambonaceids.

## Superfamily STROPHOMENACEA Schuchert, 1896

Concavo-convex or resupinate, pseudopunctate brachiopods usually with a persistent supraapical foramen which became sealed up by shell deposit in some later stocks so that mature individuals were either unattached or, exceptionally, cemented by part of the pedicle valve to a foreign body; cardinal process bilobed; pseudodeltidium sometimes completely closing the delthyrium, chilidium when present consisting of a simple convex arch. Ordovician to Carboniferous.

## Family Strophomenidae King, 1846

Strophomenaceids with a pair of simple teeth usually supported by small dental lamellae; pseudodeltidium never completely closing the delthyrium, chilidium always present; brachia lacking skeletal support but apparently consisting of a pair of very low spires exceptionally impressed on the internal shell surface. Ordovician to Carboniferous.

## Strophomeninae, n. subfamily

Strophomenids usually with a functional pedicle throughout ontogeny but sometimes lying free on the substratum due to the sealing up of the supra-apical foramen during maturity. Ordovician to Carboniferous. Type genus, *Strophomena* de Blainville.

## Leptaenoideinae, n. subfamily

Strophomenids attached throughout ontogeny by the cementation of the umbonal region of the pedicle valve to a foreign body. Middle Silurian to Lower Devonian. Type genus, *Leptaenoidea* Hedström.

*Discussion.*—The proposed family Rafinesquinidae Caster (1939) is synonymous with Strophomenidae King, 1846, as emended above. The only way to continue recognizing both families is to relegate all resupinate forms to the Strophomenidae, a patently artificial discrimination.

The adoption of secondary attachment by cementation in two strophomenid stocks (*Leptaenoidea* Hedström and *Leptaenisca* Beecher) seems to merit the division of the strophomenids into two new subfamilies. Cementation constituted a profound change of habit and was also achieved independently of this development by other strophomenoids.

## Family Stropheodontidae Caster, 1939

Strophomenaceids lacking a functional pedicle with the simple teeth and dental lamellae replaced by denticles subsequently spreading along the hinge-line; socket ridges abbreviated subsequent to the loss of dental lamellae becoming obsolescent or disappearing completely, exceptionally forming buttresses to the cardinal process lobes; pseudodeltidium initially small, apical, becoming progressively larger and in some stocks ultimately closing the delthyrium completely; chilidium initially massive becoming degenerate and in some stocks ultimately completely lost. Upper Ordovician to Upper Devonian.

## Subfamily Stropheodontinae Caster, 1939

Stropheodontids which lay free on the substratum during maturity. Upper Ordovician to Upper Devonian. Type genus, *Stropheodonta* Hall.

## Liljevallinae, n. subfamily

Stropheodontids which were attached throughout ontogeny by cementation of the pedicle valve to a foreign body. Middle Silurian. Type genus, *Liljevallia* Hedström.

*Discussion.*—The stropheodontid affinities of *Liljevallia* are revealed in the development of denticles along the hinge-line on either side of the delthyrium, the absence of dental lamellae and simple teeth, and the brachyprionid muscle scar. The stock, then, like the leptaenoideinids and the orthotetaceids is illustrative of the development of cemented forms from a number of unattached independent strophomenoid ancestors. Hitherto *Liljevallia*, *Leptaenoidea*, and *Leptaenisca* have usually been placed within the Davidsoniinae but each genus has pronounced affinities with either the Strophomenidae or the Stropheodontidae and it seems better to erect new subfamilies in the manner proposed above than to continue previous practice.

## Christianiidae, n. family

Concavo-convex strophomenaceids with a lophophore platform consisting of a pair of discrete, U-shaped loops presumably giving support to a schizolophous lophophore; pseudodeltidium and convex chilidium well developed, cardinal process bilobed, socket ridges strong; supra-apical foramen persistent throughout ontogeny. Middle and Upper Ordovician Type genus, *Christiania* Hall and Clarke.

*Discussion.*—*Christiania* represents an isolated terminal development out of one of the early strophomenoid divergences which is not closely related to any other known stock. The presence of a lophophore platform suggests affinities with the Plectambonacea, but it is more probable that the platform, which is not like any plectambonacid structure, represents an independent convergent development for in other respects and especially in the possession of a bilobed cardinal process *Christiania* is strophomenaceid.

## ORTHOTETACEA, n. superfamily

Strophomenoids without a functional pedicle; pedicle valve usually greatly modified and ce-

mented by the umbo or a greater part of the shell surface to a foreign body; brachial valve convex throughout ontogeny; cardinal process bilobed often greatly extended into the pedicle valve, sometimes highly modified; lophophore probably spirolophous in all stocks, exceptionally impressed and supported by spirally coiled calcareous ribbons. Upper Ordovician to Triassic.

## Family Orthotetidae MacEwan, 1939

Orthotetaceids with a variable but well developed hinge-line and interarea in the pedicle valve; pedicle valve consisting of one continuous chamber; pseudodeltidium of earlier stocks apical and chilidium correspondingly massive, in later stocks pseudodeltidium completely covering delthyrium, chilidium vestigial, perideltidium always present; shell surface usually finely costellate with additional radial plicae in many later stocks. Upper Ordovician to Permian.

## Subfamily Orthotetinae Waagen, 1884

Orthotetids equipped with a pair of dental lamellae often extravagantly developed and in various stages of convergence and coalescence. Upper Ordovician to Permian. Type genus, *Orthotetes* Fischer.

## Schuchertellinae, n. subfamily

Orthotetids which have lost the dental lamellae through obsolescence. Devonian to Permian. Type genus, *Schuchertella* Girty.

## Subfamily Davidsoniinae King, 1850

Orthotetids lacking costellate ornamentation; pseudodeltidium and chilidium well developed; dental lamellae obsolescent, sockets deep bounded by flaring socket ridges fused with cardinal process; both valves bear the impressions of a pair of spirally coiled brachia forming very low cones with the apices directed towards the brachial valve. Middle Devonian. Type genus, *Davidsonia* Boucharad.

*Discussion.*—The term perideltidium (Dunbar and Condra 1932, p. 67): has been given to a pair of triangular surfaces forming part of the interarea of the orthotetid pedicle valve and lying lateral to the pseudodeltidium although not necessarily adjacent to it. The perideltidium is variable in area and development but is an integral part of the interarea and is not an occurrence dependent on shell exfoliation.

Each area is slightly elevated above the rest of the interarea and in addition to being orna-

mented by growth lines parallel to the hinge-line is also feebly striated at right angles to the hinge-line so that the resultant series of grooves and ridges does not radiate from the umbo and lie obliquely to the perideltidial boundaries. Serial sections of a number of orthotetids substantiate the conclusions of Dunbar and Condra that the perideltidial boundaries are represented by a sharp deflection of both lamellar and fibrous layers. It can also be observed that the striations represent crenulations of the lamellar layer and that part of the fibrous layer adjacent to it. One would have anticipated constrictions on the hinge-line of the brachial valve corresponding to the deflected edges of the perideltidium, but none can be observed, and no plausible reason can be suggested for this differentiation of the interarea.

Apart from including the Davidsoniinae within the Orthotetidae the division of the family into two subfamilies dependent upon the presence or absence of dental lamellae is, in the opinion of the writer, more than a convenient morphological grouping for it seems to have been one of the natural consequences of orthotetid development.

The earliest known orthotetid, *Fardenia* Lamont, a biconvex form equipped with dental lamellae, appeared towards the end of the Ordovician and flourished throughout the Silurian. There is evidence to suggest (Williams, 1950, p. 120) that by the end of Silurian times sufficient divergence had occurred within the stock to give rise to a schuchertellid, which had lost the dental lamellae by obsolescence, and also a concavo-convex Schellwienella (like the Lower Devonian *S. umbraculum* (Schloth.)) with strongly developed divergent dental lamellae.

It is probable that two such forms were ancestral to two main stocks, viz, orthotetimid and schuchertellimid which remained independent during their subsequent histories. The range of all described genera is consistent with this belief and there is no evidence to suggest that either stock was replenished from the other by

obsolescence of the dental lamellae or the development of secondary ones.

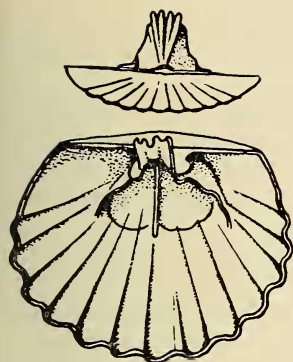
With regard to the various genera equipped with well-developed dental lamellae it is noteworthy that the disposition of the lamellae seems to be closely related to the configuration of the pedicle valve. Thus Schellwienellas possess concave pedicle valves and divergent dental lamellae while all other orthotetimidids have convex pedicle valves and dental lamellae which are parallel, convergent, or in various stages of coalescence. Taking into consideration the fact that the dental lamellae always occupied a constant position relative to the interarea, where they lay immediately beneath the teeth, it is reasonable to assume that their disposition was a function of the form and growth of the anterior wall of the pedicle valve. Consequently many species ascribed to such genera as *Sicelia*, *Orthotetina*, *Geyerella*, and *Meekella* may represent independent convergences rather than closely related stocks.

#### Gemmellaroïidae, n. family

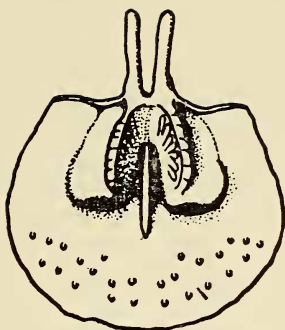
Attached orthotetaceids with a long conical pedicle valve capped by a reduced operculiform brachial valve; hinge-line obsolescent, interarea completely lost except for a narrow elevated ridge in the pedicle valve representing the pseudodeltidium; articulation aided by the development in both valves of an excessively thickened margin serrated by oblique furrows; cardinalia massive, elongated, with the bilobed cardinal process and laterally extended socket ridges completely fused, in the interior of the pedicle valve the cardinalia is contained within a subcircular myophore chamber, about a third the length of the valve extending from the umbo almost to the periphery of the valve and lying immediately anterior to the pseudodeltidium; fibrous layer of shell adjacent to lamellar layer disposed in long sharp folds radiating from the umbo. Permian. Type genus *Gemmellaroia* Crossman.

FIGS. 8-12.—8, Orthotetimid morphology, *Meekella* White and St. John; interior of brachial valve (8a) with posterior view above; interior of pedicle valve (8b). 9, Scacchinellid morphology as typified by *Scacchinella* Gemmellaro; interior of brachial valve (9a); reconstruction of part of the pedicle valve interior (9b) showing the median septum and the transverse partitions. 10, Gemmellaroïid morphology as typified by *Gemmellaroia* Crossman; complete shell with a transverse section of the pedicle valve to show the shell structure and the disposition of the myophore chamber (10b), anterior view of brachial valve interior (10a). 11, Thecospirid morphology as typified by *Thecospira* Zugmayer; interior of brachial valve (11a), interior of pedicle valve (11b) tilted to show the muscle scar arrangement. 12, Diagrammatic representation of the interarea of the orthotetid pedicle valve to show the nature of the perideltidium (PE); lamellar layer (L), fibrous layer (F), pseudodeltidium (P), tooth (T).

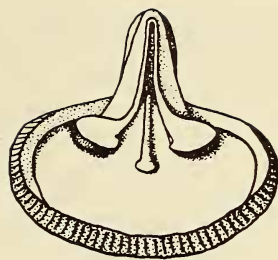




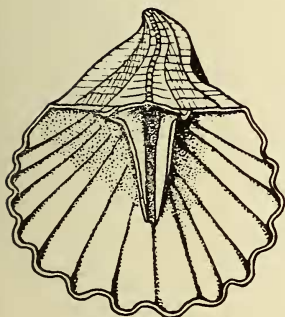
8a



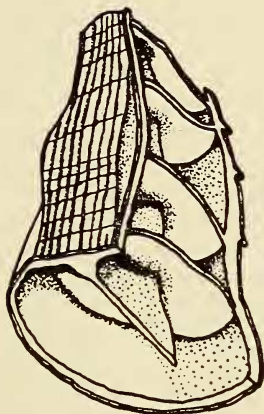
9a



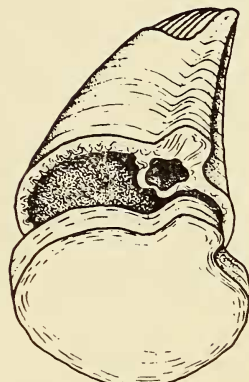
10a



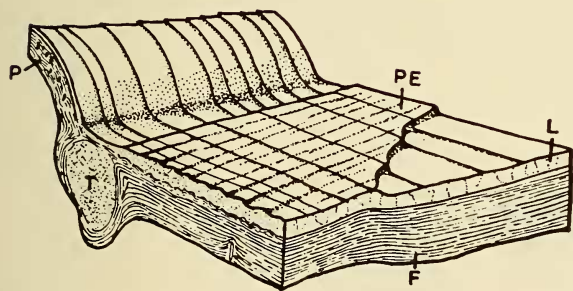
8b



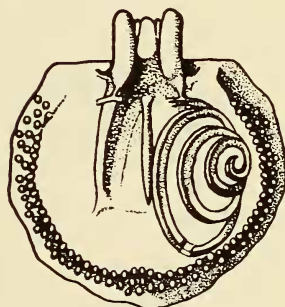
9b



10b



12



11a



11b

Figs. 8-12 (See opposite page for legend).

*Discussion.*—The gemmellaroïds represent a later divergence from a more generalized orthotetid stock in which a number of morphological modifications present in the orthotetids generally are carried to conclusion. Thus the excessive elongation of the pedicle valve and the reduction of the hinge-line is seen in late orthotetids like *Orthotetina* but never on the scale of the gemmellaroïds. The myophore chamber is especially characteristic of the family but is not unique for a similar structure evolved in an otherwise typical Permian orthotetid (*Orthotetella* King).

Scacchinellidae, n. family

Attached orthotetaceids, pedicle valve long, conical twisted with longitudinally striated interarea, brachial valve gently convex, exterior spinose without radial ornamentation; interior of pedicle valve with a strong median septum extending anteriorly for over half the length of the shell and divided into a series of chambers by the deposition of a variable number of transverse partitions the last formed chamber presumably being the only one occupied by the viscera; brachial valve with a long bilobed cardinal process which extended well into the pedicle valve on either side of the median sep-

tum; socket ridges small, adductor muscle scars impressed on the inner surfaces of a pair of long, thick ridges extending anteriorly from the cardinal process bases. Permian. Type genus, *Scacchinella* Gemmellaro.

*Discussion.*—The scacchinellids are unique among the orthotetaceids and indeed among all brachiopods in the division of the pedicle valve into a series of chambers by the deposition of transverse partitions. The writer has observed in an occasional *Derbyia* the apparently natural occurrence of thin flaps of fibrous shell deposit projecting into the body chamber and a similar occurrence is reported by Licharew (1928, p. 272) in the gemmellaroïd *Tectarea*. But in the scacchinellids the partitions were apparently a regular feature of all mature individuals and were presumably a consequence of the great disparity between the volume of the soft parts and the excessive elongation of the pedicle valve.

Family Thecospiridae Bittner, 1893

Orthotetaceids attached to a foreign body by cementation of the pedicle valve, exterior tuberculate without radial ornamentation but sometimes rugate; interarea of pedicle valve entire, without any definition of the pseudodeltidium, interarea of brachial valve vestigial,

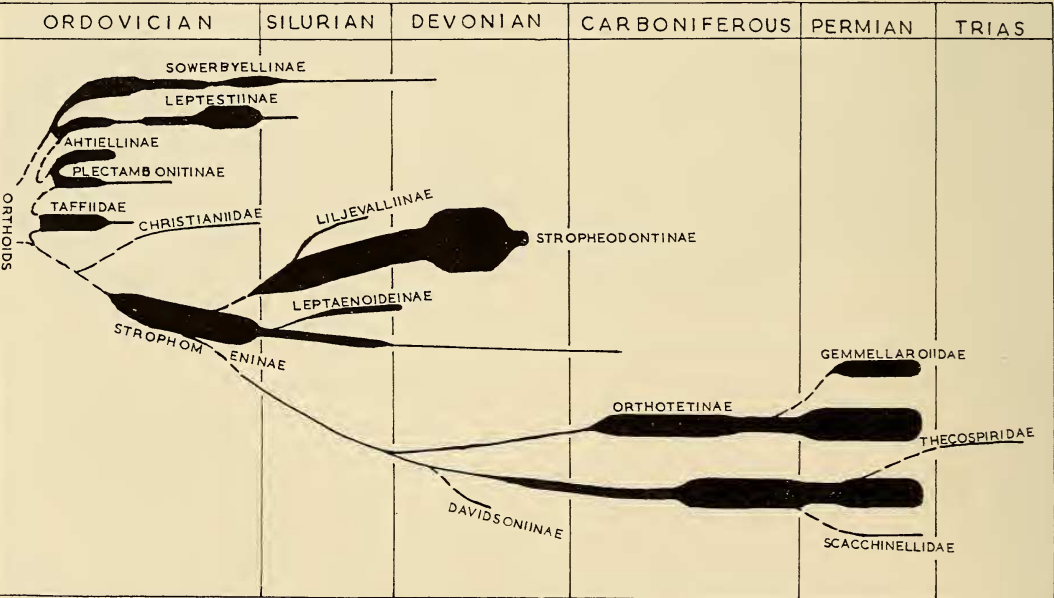


FIG. 13.—The stratigraphical distribution of the strophomenoid brachiopods, including the theci- deids; the size of the suprageneric categories figured in the chart is proportionate to the number or genera included in each category as well as their stratigraphical range.

childium absent; pedicle valve with strong unsupported teeth and a small broad muscle scar divided medianly by a low median septum; brachial valve with an erect cardinal process, functionally bilobed but united medianly to form a tripartite structure, sockets deep, muscle scars contained within a pair of subparallel ridges extending anteriorly from the cardinalia and divided medianly by a low median ridge; cardinal process bases prolonged into a pair of short processes which support a pair of spirally coiled calcareous ribbons directed towards the lateral slopes of the pedicle valve; brachial ribbon sharply folded throughout its length to give a V-shaped cross section. Triassic. Type genus, *Thecospira* Zugmayer.

*Discussion.*—The orthotetaceid features of *Thecospira* are so striking and numerous that it cannot be excluded from the strophomenoids because its lophophore was supported by a pair of spirally coiled calcareous ribbons. The shell is strongly pseudopunctate, the spicules penetrate the internal surfaces which are tuberculate and though they do not penetrate the lamellar layer they are excessively prolonged to give the exterior a bluntly spinose appearance. Other strophomenoid features include the mode of attachment, the entire interarea of the pedicle valve (compare the stropheodontids and a similar tendency in those orthotetaceids with a vestigial chilidium) the cardinal process and the muscle scars which are reminiscent of late orthotetaceids like *Derbya*.

The presence of calcified spiral supports in *Thecospira* then does not signify that the stock was related to the rostrospiroids or spiriferoids; they represent an independent development out of a spirolophous orthetetaceid.

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PALEOBOTANY. —*Prosseria grandis*, a new genus and new species from the Upper Devonian of New York.<sup>1</sup> CHARLES B. READ, U. S. Geological Survey. (Communicated by Roland W. Brown.)

The extensive collections of fossil plants made by C. S. Prosser from Devonian horizons in New York and Ohio contain numerous specimens of interest to students of Paleozoic floras. One of the most remarkable of these specimens is a large slab of black shale and its counterpart carrying as an incrustation the remains of an unusual representative of the Articulatae. The literature on Devonian floras contains no reference to any genus that may be extended to include this plant. In consequence this fossil

is referred to a new genus, *Prosseria*, named in honor of the collector. There follows a discussion of the type specimen and its possible relationships.

PTERIDOPHYTA  
 Articulatae  
 ?Pseudoborniales

*Prosseria*, n. gen.

Generic characters at present defined by the single known species.

*Prosseria grandis*, n. sp.

*Diagnosis.*—Plant large, stem 25 mm in di-

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey.